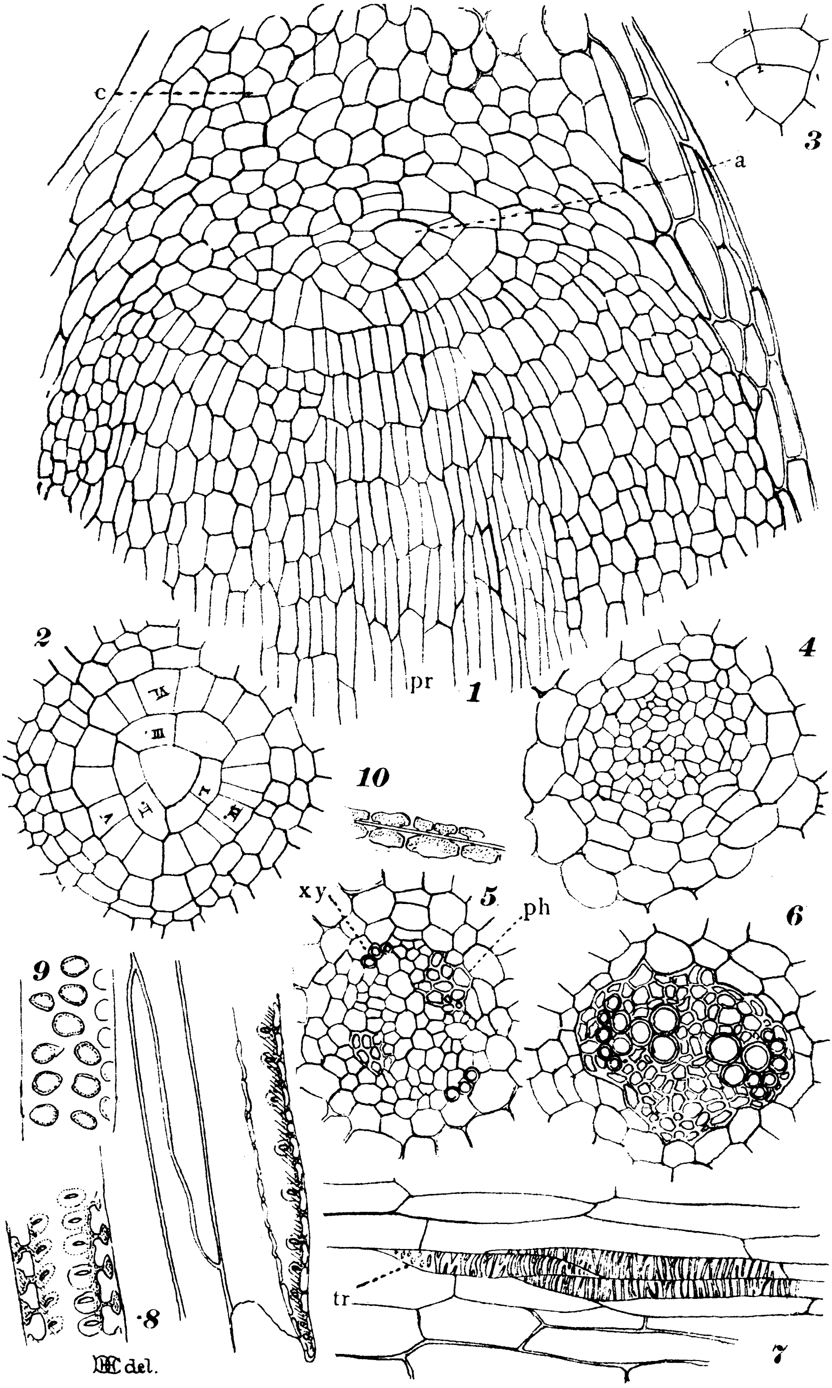

CAMPBELL ON BOTRYCHIUM.

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The Development of the Root in Botrychium ternatum.

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(WITH PLATE IV.)

Among the peculiarities of the Ophioglossaceæ distinguishing them from the true ferns are the roots. These are much less numerous, but of correspondingly greater size, only one root being developed at the base of each leaf, and consequently, in such forms as produce but one leaf annually, but one principal root is formed each year, though probably several leaves are developed the first year, and a corresponding number of roots. On account of the extreme shortening of the internodes of the stem, which in large specimens of the species under consideration seldom reaches a length of more than two or three centimeters, the roots are much crowded.

The roots are thick and fleshy, and almost completely destitute of root-hairs, thus differing very much from most other pteridophytes, the older ones being sometimes 3mm. in diameter. They have a thin brown epidermis in the younger parts, becoming in the older portions thicker and wrinkled, forming with the underlying tissue a tough and ridged cortex.

Arising from the larger roots are smaller ones, formed in acropetal succession, but in smaller numbers than in the true ferns, and not as distinctly two-ranked. Nothing was observed to indicate that they arose dichotomously, or in any way differently from the ordinary methods in other pteridophytes. In some cases it was evident that a lateral root had taken the place of the main one, whose apex had apparently been in some way injured, and in one case this had been repeated, two roots branching out the second time nearly at the same point, diverging widely, and at first sight having the appearance of dichotomous branching, but their lateral origin was plainly evident on closer examination. Possibly the supposed dichotomous branching of the roots was inferred from some such cases. Occasionally where secondary roots were developed very early, they also gave rise to lateral rootlets, but this was not very common.

Longitudinal sections through the conical end of the root show a very early division of the young tissues, which a short distance below the apex becomes very conspicuous. The growth is due to the division of an apical cell of the usual form, whose derivative cells become differentiated into the permanent tissues of the root. The root-cap differs in appearance from that of the

true ferns in the indistinctness of the layers of cells representing the successive segments of the apical cell, all traces of the stratification so conspicuous in true ferns being very early lost. Occupying the center of the root is a cylinder of procambium cells, and surrounding this, several rows of broader cells, with intercellular spaces between their lateral walls. On account of the air occupying the spaces, this zone of cells is very conspicuous when the section is mounted in water. Lying outside of these cells is a second zone of smaller cells destitute of intercellular spaces, and surrounding the whole is the epidermis whose cell-walls, very early, become brown in color, and form a continuous thin brown covering over the end of the root. Some of the cortical cells lying immediately underneath later have their walls similarly changed.

The apical cell (figure 1. *a*) is a nearly equilateral tetrahedron in form, and the succession of segments seems to be perfectly regular. Each segment is formed by a wall parallel to one of the faces of the apical cell, the cell thus formed being tabular, with the broader faces triangular. The cap-cell is the last formed of each cycle of segments, and differs in its subsequent divisions from the three lateral segments. Each of the latter is first divided into two nearly equal cells by a radial wall (figure 2. *a*). In each of the cells thus formed a tangetial wall arises, dividing it into an inner and an outer cell, the former being the larger; and very soon after, the inner cell becomes further divided by a second tangential wall into two nearly equal cells. Of the three cells into which each half of the original segment is now divided, the inner one gives rise to the central procambium cylinder of the root; the middle one to the ground tissue lying next the procambium, and probably to the whole, or at any rate to a large part of the cortical parenchyma; from the outer cell, the epidermis and possibly part of the cortical tissue. I was unable to determine positively whether or not the outer cell underwent any further division by walls parallel to the first wall, that is, whether the cells derived from this outer cell formed more than one layer, or whether all the subsequent division walls were perpendicular to that first formed.

In the segments from which the root-cap is formed, the first wall, as seen from above (figure 3. I), is parallel to one of the sides of the triangular cell, dividing it into two unequal cells, an elongated four-sided, and a triangular one. The former is divided into two by a wall perpendicular to the first (figure 3. II), before the other is divided. For a short time walls are formed only at right angles to the broad faces of the segment, as

in true ferns. In the latter this remains permanent, so that the root-cap consists of a series of distinct strata or lamellæ, each composed of a single layer of cells, and representing a single segment of the apical cell; but in Botrychium walls are soon formed in all directions, and thus the original strata become so merged as to obliterate completely the boundaries between them.

In the lateral segments there are formed for some time walls perpendicular to the broad faces only of the segments, so that the latter remain for some time single layers of cells, the growth of the segments being almost entirely lateral, and the vegetative cone is thus rendered very obtuse. The first transverse walls are formed in the outer cells, where they continue to form rapidly, alternating with longitudinal walls and forming a small-celled tissue whose cells are nearly cubical in form. Division does not occur so rapidly in the cells lying nearer the central part of the root, and these are consequently of larger size; they also very early show intercellular spaces. Those lying immediately in contact with the procambium cells of the central cylinder are narrower than the others and form the bundle-sheath, which, however, never becomes very sharply differentiated.

The tissue derived from the innermost cells of the segments is composed of cells whose transverse divisions are very few as compared with the longitudinal ones, and are therefore long and narrow, this becoming very early marked and sharply separating the central plerome cylinder from the surrounding tissues. The transverse partitions are usually oblique so that the cells have more or less pointed ends, forming the procambium (figure 1. *pr*). All of the young cells possess a large central nucleus from which radiate protoplasmic threads, which with the peripheral protoplasm of the cells contain numerous granules.

The root soon reaches nearly its full diameter, any further growth being due to increase in the size of the cells, and longitudinal divisions cease, although for some time transverse walls form rapidly except in the procambium cells. These finally cease and the subsequent lengthening of the root is due to the elongation of its cells.

The epidermal cells become thicker walled, the walls at the same time becoming brown, and the cells losing the greater part or all of their contents.

The ground-tissue cells remain distinguishable into two portions, although this is not so evident as in the younger parts of the root. They develop great quantities of starch in small, roundish or oval granules, these being especially numerous in the larger celled inner parenchyma.

The development of the different parts of the fibro-vascular bundle is most readily followed by means of a series of transverse sections. Such a section, made before any of the permanent tissue is formed, shows that the young bundle is composed of a mass of thin-walled cells whose diameter is very much less than that of the surrounding ground-tissue cells, so that the young bundle is clearly defined (figure 4).

The first indication of the formation of permanent tissue is a change in the walls of certain cells arranged in groups at the periphery of the cylinder and at equal distances from each other (figure 5. *ph*). Their walls become noticeably thicker and strongly refractive, so that they are easily recognized. These cells form the beginning of the phloem masses of the complete bundle. Shortly after the first phloem cells have become differentiated, there are formed at equal distances from them, also at the outside of the bundle, an equal number of groups, consisting at first of two or three cells, whose walls become strongly thickened, but appear opaque, so that they differ markedly from the phloem cells. These are the primary tracheids and form the beginning of the xylem (figure 5. *xy*).

A longitudinal section of a bundle at this stage shows that the primary tracheids are narrow pointed cells, with spirally thickened walls, the spirals more or less confluent so as to form reticulate markings (figure 7. *tr*).

The further development of the bundle proceeds very slowly, the formation of permanent tissue continuing from the points at the circumference toward the center. The secondary tracheids, for there are no true vessels, are frequently marked with bordered pits, resembling more those of gymnosperms than the scalariform markings of the vessels of ferns. Their formation can be readily followed by making thin longitudinal sections at points where the bundle is not fully formed.

These markings begin by the thickening of the wall leaving spaces of considerable size where the wall remains of its original thickness. At this stage (figure 9), the wall appears marked with large but shallow pits. As the thickening progresses, while the bottom of the pit retains its original diameter, the parts of the wall surrounding it grow over it so as to make the pit assume more and more the form of an inverted cone. The upper opening does not close up, but after it has reached a certain size its walls cease to approach each other and the upper part of the pit has the form of a short tube, so that the whole pit is like an ordinary inverted funnel. On account of the uniform diameter of the neck of the funnel, its outline, when seen from above,

is very sharply defined; whereas the outline of the base is much fainter, and the whole pit seen from above appears as a very definite pit whose transverse diameter is the greater, surrounded by a much less distinct, but usually quite evident circle marking the original outline of the pit (figures 8 to 10). In proportion as the pits are more or less elongated and crowded, the tracheid approaches more those of the ferns or gymnosperms. I could not certainly determine whether or not the bottom of the pit was finally absorbed. There is a general correspondence in the place of formation of pits on the adjacent walls of neighboring tracheids, but not so marked as is often the case. Sometimes the thickening of the wall is uniform between the pits, so that they retain the form of unbordered pits.

The bundles differ in form in the main and lateral roots. In the former the mature bundle has a nearly triangular section, the xylem consisting of three radially placed oval masses of tracheary tissue, with three masses of rather thick-walled, imperfectly developed sieve tissue, constituting the phloems lying between. The limits of the phloem masses are not very clear, merging more or less into the thin-walled parenchyma, constituting the rest of the fibro-vascular cylinder. In the lateral roots the bundle is oval in outline and the xylem and phloem in two masses instead of three (figure 6). In neither case do the separate masses coalesce. In one case a very strong main root showed four instead of three xylem and phloem masses.

The phloem consists of elongated cells of varying diameter, some of the larger ones with the transverse walls only slightly oblique, probably being undeveloped sieve-tubes. The rest of the cells are narrower, with much more oblique walls, so that their ends are often decidedly pointed; otherwise they differ but little from the surrounding parenchyma.

EXPLANATION OF PLATE IV.—Fig. 1. Longitudinal section through the apex of a main root of *Botrychium ternatum*. × 150. *a*, apical cell. *pr*, procambium cylinder. *c*, root-cap.

Fig. 2. Transverse section through the region of the apical cell. × 150. The first six lateral segments are numbered.

Fig. 3. Young segment of root-cap, showing the first division walls, I and II. × 245.

Figs. 4–6. Transverse sections through the young bundle of a lateral root. 6 is practically complete. *ph*, phloem. *xy*, xylem. × 245.

Fig. 7. Longitudinal section of the bundle of a main root, of about the age of Fig. 6, showing the primary tracheids, *tr*. × 245.

Fig. 8. Longitudinal section through mature bundle of main root, showing parts of two complete tracheids. × 500.

Fig. 9. Surface of the wall of a young tracheid, showing the early stages of the bordered pits. × 500.

Fig. 10. Section through the wall separating two tracheids with bordered pits. × 500.